REVIEW

Interactions of transgenic *Bacillus thuringiensis* insecticidal crops with spiders (Araneae)

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Abstract. Genetically modified crops expressing insecticidal proteins from *Bacillus thuringiensis* (Bt) have dramatically increased in acreage since their introduction in the mid-1990's. Although the insecticidal mechanisms of Bt target specific pests, concerns persist regarding direct and indirect effects on non-target organisms. In the field, spiders may be exposed to Bt toxins via multiple routes, including phytophagy and pollenivory, consumption of Bt-containing prey, and soil exudates in the detrital food web. Beyond direct toxicity, Bt crops may also have indirect impacts, including pleiotropic and prey-mediated effects. Here, we comprehensively review the literature and use meta-analyses to reveal that foliar spider abundance is unaffected by Bt corn and eggplant, while cotton and rice revealed minor negative effects and there were positive effects from potato. Moreover, the soil-dwelling community of spiders was unaffected by Bt corn and cotton, while positively impacted in potato. However, Bt crops had higher populations of both foliar and epigeal spiders than insecticide-treated non-Bt crops. The current risk-assessment literature has several caveats that could limit interpretations of the data, including lack of taxonomic resolution and sampling methods that bias the results in favor of certain spiders. These families responded differently to Bt crops, and spider responses to insecticides are species- and toxin-specific, thus highlighting the need for greater taxonomic resolution. Bt crops have become a prominent, and increasingly dominant, part of the agricultural landscape; understanding their interactions with spiders, a diverse and integral component of agroecosystems, is therefore essential.

Keywords: Spiders, genetically modified organisms, GMO, non-target risk-assessment, agroecosystem, Bt toxin

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1. INTRODUCTION

The adoption of biotechnology in agriculture has been employed in the global push toward sustainable intensification of crop productivity, in an attempt to meet demands for increased food security for a growing worldwide population. The planting of genetically modified crops has been widespread; in 2009, 135 million hectares of biotech crops were grown by an estimated 14 million farmers in 25 countries (James 2009). Insect-resistant genetically modified crops (e.g., *Bacillus thuringiensis* [Bt] crops) have become dominant fixtures in many of the world's agricultural regions (James 2007; Naranjo 2009). The replacement of conventional crops with their Bt counterparts is thereby altering the composition and dynamics of agroecosystems across regional and global scales.

Bt crops are genetically engineered to express insecticidal proteins of the entomopathogen *Bacillus thuringiensis* Berliner 1915 (Bacillales: Bacillaceae). Transgenic plants are modified by inserting a gene from *B. thuringiensis* into the genome of the crop plant, termed a transgenic event, thereby allowing the crop to express insecticidal proteins in its own tissues. The insecticidal proteins expressed in these transgenic crops are known as Bt δ-endotoxins/Cry proteins. The insecticidal mode of action occurs when Bt toxins are ingested by insect pests; these proteins bind to receptors on the midgut lining of susceptible individuals, causing lysis of epithelial cells on the gut wall and perforations in the midgut lining, which stops feeding and causes death by septicemia (Glare & O'Callaghan 2000). Bt toxins target a fairly narrow spectrum of pest insects that possess specific physiological traits (i.e., gut pH and toxin receptor sites in the midgut) and thus intuitively pose less risk to non-target species than broad-spectrum insecticides (Marvier et al. 2007; Wolfenbarger et al. 2008; Naranjo 2009; Duan et al. 2010). For example, Cry1 proteins are effective against certain lepidopterans, and Cry3 proteins affect certain coleopterans. Despite the relative safety in comparison to conventional insecticides and economic benefits to growers (Hutchinson et al. 2010), there is still concern that Bt crops could have non-neutral interactions with non-target organisms, such as spiders.

Current risk-assessment literature has focused on the direct and indirect effects of transgenic Bt crops on a variety of non-target taxa, including important arthropod predator groups such as ladybird beetles (Coleoptera: Coccinellidae) (e.g., Lundgren & Wiedenmann 2002; Harwood et al. 2007), ground beetles (Coleoptera: Carabidae) (e.g., French et al. 2004; Zwahlen & Andow 2005; Duan et al. 2006; Harwood et al. 2006; Peterson et al. 2009), lacewings (Neuroptera: Chrysopidae) (e.g., Hilbeck et al. 1998; Dutton et al. 2002; Guo et al. 2008), and true bugs (Hemiptera) (e.g., Al-Deeb et al. 2001a; González-Zamora et al. 2007; Duan et al. 2007). Within the arachnids, non-target studies have focused primarily on predatory mites (Acari: Phytoseiidae), and the majority of

these studies have found no negative impacts of Bt toxins (e.g., Obrist et al. 2006a; Esteves et al. 2010). In contrast to the abundant risk-assessment literature addressing predatory mites, spiders have received a particularly low level of attention in proportion to their importance in cropping systems.

Therefore, this review will address the interactions between Bt crops and spiders in transgenic agroecosystems, forming a framework for risk-assessment by reviewing the role of spiders in agroecosystems and the direct and indirect routes by which Bt crops may affect spider communities. Subsequently, literature examining the consequences of this exposure to Bt toxins for spider fitness and fecundity is reviewed. Additionally, the effects of Bt crops at the community level, as measured by abundance of foliar and soil-dwelling spiders in the field, are evaluated using meta-analysis to examine both crop- and family-specific effects. A discussion of the literature reviewed will address limitations of these studies and implications of spider responses to chemical insecticides for Bt crop risk-assessment. This review provides a synthesis of field- and laboratory-based studies of the impacts of *Bacillus thuringiensis* crops on the diverse and agriculturally significant spider community.

2. ROLE OF SPIDERS IN AGROECOSYSTEMS

As generalist predators, spiders have often been overlooked in the context of biological control of insects (DeBach & Rosen 1991; Hoy 1994), despite their ubiquitous nature and high abundance in agricultural fields (Riechert & Lockley 1984). However, generalist predator species assemblages can significantly reduce pest populations in many cases (reviewed by Symondson et al. 2002). Polyphagous habits may allow some predators to survive the high levels of disturbance in agricultural settings (Murdoch et al. 1985), meaning that generalists are often the principal predators in annual crops.

2.1 Prevalence of spiders in croplands.—Indeed, spiders often dominate the agroecosystem, in part due to their ability to reach high population densities. Nyffeler & Sunderland (2003) reported 2–600 spiders per m^2 in European field crops, consisting primarily of linyphiids, while only 0.02–14 spiders per m^2 were found in North American annual crops. However, recent studies have found higher population densities in the USA: 19 spiders per m^2 on the soil surface in annual field crops in Illinois, (Lundgren et al. 2006) and an average of 67 spiders per m^2 on the soil surface in early season field corn in South Dakota, (Lundgren & Fergen, in press). Spider communities in agroecosystems can also be very diverse; over 600 combined species of spiders were found across nine field crops in U.S. agriculture (Young & Edwards 1990). Spiders represent a major portion of the invertebrate predators found in terrestrial ecosystems, and their populations often outnumber other predatory arthropods in a diversity of habitats.

2.2 Biological control potential.—Spiders are capable of capturing a significant proportion of the insects in the trophic level below them, as well as at their own trophic level (Wise 1993). For example, spiders are responsible through direct predation and non-consumptive effects for a reduction of up to 42% of pest cutworm larvae in tobacco (Nakasuji et al. 1973) and 49% of pest aphid populations in cereal crops in the United Kingdom (Chambers & Aikman 1988). Thus, spiders, in conjunction with other natural enemies present within agroecosystems, can exert a positive synergistic effect on pest population dynamics (Sunderland et al. 1997). Additionally, spiders are more likely to remain in agroecosystems during periods of low prey abundance than to disperse to surrounding areas (Greenstone 1999), allowing for greater predation on prey species once they enter a cropping system. Spiders also exert synergistic biological control effects via partial consumption of caught prey (Haynes & Sisojevic 1966; Samu 1993) or without consumption by dislodging pests from plant surfaces (Nakasuji et al. 1973; Mansour et al. 1981), causing mortality in webs (Nentwig 1987; Alderweireldt 1994), altering pest behavior via predation risk (Schmitz et al. 1997) and "superfluous killing" (Provencher & Coderre 1987; De Keer & Maelfait 1988; Mansour & Heimbach 1993; Samu & Biro 1993; Maupin & Riechert 2001) (reviewed by Sunderland 1999). Linyphiidae in particular are known to build their webs selectively at micro-sites with high prey density and diversity (Harwood et al. 2001, 2003; Harwood & Obrycki 2007; Romero & Harwood 2010). Agrobiont spider species (reaching high dominance in agroecosystems [Samu & Szinetár 2002]), display a number of life history traits allowing them to persist in annual agroecosystems despite frequent disturbances and periods of prey scarcity, including high egg production, an extended breeding season, multiple generations per year, the ability to immigrate into annual crops early in the season via ballooning, and low metabolic rates (Anderson 1970, 1996; Greenstone & Bennett 1980; Anderson & Prestwich 1982; Bishop & Riechert 1990; Nyffeler & Breene 1990; Schmidt & Tscharntke 2005). These life history traits make linyphiids important biological control agents and a major component of ecological webs in agroecosystems (Thorbek et al. 2004).

Spiders may also contribute to biological control efforts if these generalist predators are able to move into a cropping system early in the season (Sunderland et al. 1997). The ballooning ability of spiders, particularly Linyphiidae, which can exhibit this behavior at both immature and adult stages (Weyman et al. 1995), allows these predators to rapidly colonize a cropping system following cultivation of the field (Riechert & Lockley 1984; Sunderland et al. 1986). Spiders can then build their populations by subsisting on alternative non-pest prey or non-prey resources before pests arrive; this 'lying in wait' strategy may allow the predators to exert significant control over the pest population and even drive it to extinction (Murdoch et al. 1985). For example, in winter wheat in the United Kingdom, Collembola are an abundant alternative prey resource for linyphiid spiders early in the growing season (Harwood et al. 2003); the presence of this alternative food resource maintained spiders in the field and allowed for greater predation rates on pest aphids when their populations increased later in the growing season (Harwood et al. 2004). Similarly, Settle et al. (1996) found populations of generalist

predators in rice were supported early in the season by detritivorous alternative prey.

2.3 Importance of diverse spider assemblages.—Although individual spider species do not exert significant biological control on agricultural pests, the multi-species spider assemblages found in agroecosystems can provide valuable suppression of pest populations (Greenstone 1999). Spider assemblages can cause mortality of nearly all life stages of an agricultural pest due to their variation in foraging behavior, diel activity, microhabitat selection, and size across species. Spiders found within agroecosystems occupy a wide range of ecological niches, which often leads to the grouping of spiders displaying similar foraging behaviors into guilds (Uetz 1977; Post & Riechert 1977; Uetz et al. 1999). However, within these guilds finer taxonomic resolution may yield differences in prey resource utilization (e.g., the subfamilies Erigoninae and Linyphiinae [Harwood et al. 2003]).

3. ROUTES TO EXPOSURE

Bt crops may affect non-target species residing within higher trophic tiers in two ways: via direct effects of the toxin following ingestion and/or via changes to the structure of agroecosystems that are associated with the widespread adoption of Bt crops (Lundgren et al. 2009a). Depending on the gene promoter that is used in a particular transgenic event and crop, the insecticide's final distribution and concentration within the plant may include any of a variety of tissues and exudates, including root and vegetative tissue, flowers, nectar, or pollen (Shi et al. 1994; Hilder et al. 1995; Rao et al. 1998; Couty et al. 2001; Raps et al. 2001; Bernal et al. 2002a; Wang et al. 2005; Wu et al. 2006; Burgio et al. 2007). Combined with their diversity and generalist feeding habits, routes to exposure are potentially complex for spiders (Fig. 1).

3.1 Consumption of pollen.—Bt proteins are often present in crop pollen and other plant tissues. Feeding directly on pollen, or on silk that has intercepted pollen, present direct routes of exposure to Bt toxins. Concentration of insecticidal Bt proteins in pollen varies depending on the crop type, transgenic event, and phenology, as well as factors of the region and environment (Fearing et al. 1997; Duan et al. 2002; Grossi-de-Sa et al. 2006; Obrist et al. 2006b). Pollen is a component of the diets of some generalist predators, including spiders; a pollen-based diet can increase spiderling survival of select groups, including a crab spider *Thomisus onustus* Walckenaer 1805 (Thomisidae) (Vogelei & Greissl 1989) and an orb-web spider *Araneus diadematus* Clerck 1757 (Araneidae) (Smith & Mommsen 1984). Orb-web spinning spiders located inside or around the borders of transgenic cornfields could also potentially consume Bt proteins from pollen blown by wind onto their webs. Despite its large size and typically rapid settling rate, corn pollen may travel up to 30 m from its source (Raynor et al. 1972). Pollen deposition can reach high levels in cornfields and their margins: 1,400 grains/cm^2 on milkweed leaves (Pleasants et al. 2001) and over 200 grains/cm^2 in simulated linyphiid spider webs (Peterson et al. 2010). For spiders that re-ingest their webs in order to recycle the silk and rebuild their webs daily (e.g., some araneids), this behavior could facilitate the ingestion of pollen that dusted their webs during anthesis (Ludy 2004; Ludy & Lang 2006a). The sheet-web weaving spiders (Linyphiidae) readily consume
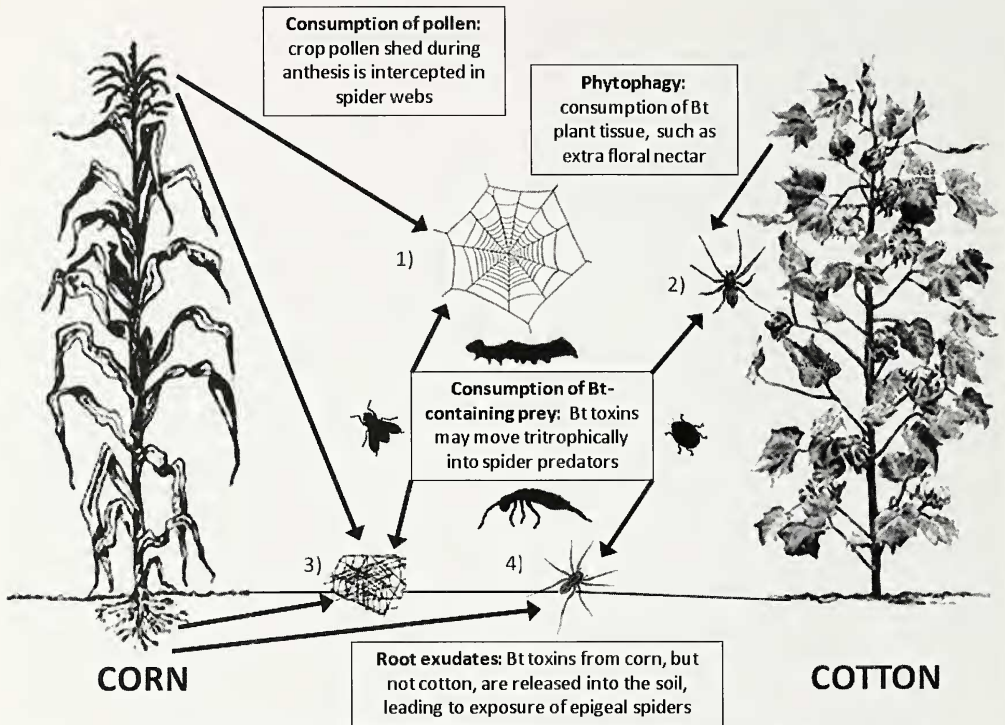
Figure 1.—Potential routes to Bt toxin exposure for spiders in transgenic agroecosystems. Sources and pathways for Bt toxin movement are highlighted for several spider families common in transgenic corn and cotton agroecosystems, including 1) Araneidae, 2) Anyphaenidae, 3) Linyphiidae, and 4) Lycosidae.

pollen that has been intercepted in their webs (Sunderland et al. 1996; Peterson et al. 2010). The combination of high pollen deposition and low prey interception rates at ground-based linyphiid webs in transgenic corn maximizes the potential for pollen consumption and uptake of Bt toxins (Peterson et al. 2010). Thus, there is considerable exposure to pollen in many agroecosystems over a very short window of time (during anthesis), which may constitute a significant route to exposure to Bt toxins.

3.2 Other forms of phytophagy.—Many non-target species, including beneficial insects and spiders, rely on plant-based foods (reviewed by Wäckers 2005 and Lundgren 2009) and thus are at risk of being affected by Bt toxins, as toxin transfer can be facilitated by direct consumption of Bt-containing plant material (Dutton et al. 2002; Meissle et al. 2005; Obrist et al. 2005, 2006a, c). Despite the reportedly wide dietary breadth of spiders (Nyffeler et al. 1994), they are traditionally considered a strictly predaceous group. However, recent studies have shown the propensity of some spiders to utilize plant food resources, such as *Bagheera kiplingi* Peckham & Peckham 1896 (Salticidae) consuming the Beltian bodies of the acacia tree (Meehan et al. 2009) and several species of both the

genus *Cheiracanthium* (Miturgidae) and *Hibana* (Anyphaenidae) consuming extra-floral nectar (Patt & Pfannenstiel 2008, 2009; Taylor & Pfannenstiel 2008, 2009; Taylor & Bradley 2009). Therefore, ingestion of plant material represents a potential pathway to Bt toxin exposure of non-target spiders in transgenic agroecosystems, although feeding frequency on plant resources (other than pollen) in transgenic crops has not been documented.

3.3 Consumption of Bt-containing herbivores or other prey.—Spiders may be exposed to Bt toxins through the consumption of prey that have fed on Bt tissue. Trophic linkages between spiders and prey can vary, based on the predator's foraging mode; aerial prey, such as Diptera, are of high importance to Tetragnathidae and less important to Lycosidae and Linyphiidae, while the opposite pattern of trophic strength is seen for Collembola, with this prey playing the largest role in the diet of linyphiids (Nyffeler & Sunderland 2003) and juvenile lycosids (Wise 1993; Oelbermann et al. 2008). Spiders in a transgenic agroecosystem are therefore likely to intercept and consume a potentially wide variety of prey, which may have been exposed to Bt toxins through their diet. Spiders are capable of consuming potentially Bt-containing prey items in

agricultural fields, such as seen in the trophic linkages between spiders and western corn rootworm *Diabrotica virgifera virgifera* LeConte (Coleoptera: Chrysomelidae) (Lundgren et al. 2009b). Additionally, secondary predation of smaller arthropod predators that contain Bt toxins may occur; some small, soft-bodied predatory insects, such as *Nabis roseipennis* Reuter 1872 (Hemiptera: Nabidae) and *Orius insidiosus* (Say 1832) (Hemiptera: Anthocoridae) show high uptake of Bt toxins in the field (Harwood et al. 2005) and could easily become prey to spiders.

3.4 Root exudates and the detrital food web.—Another potential route of transgenic protein movement to spiders is through the soil-based food web and ingestion of soil-dwelling arthropods via root exudates and plant biomass. Bt corn, potato, and rice all release transgenic protein-containing root exudates during plant growth; however, Bt canola, cotton, and tobacco do not (Saxena et al. 1999, 2004; Saxena & Stotzky 2000; Icoz & Stotzky 2007). Several studies have quantified the persistence of Bt toxins in the soil (Koskella & Stotzky 1997; Saxena et al. 2002; Zwahlen et al. 2003a; Stotzky 2004; Icoz & Stotzky 2008), with results indicating that Bt toxins will persist in the soil from 2–32 wk. This wide discrepancy in persistence times may be partially due to differences in microbial activity (Palm et al. 1996; Koskella & Stotzky 1997; Crecchio & Stotzky 1998), which is in turn affected by the pH and mineral content of soils (Icoz & Stotzky 2008). Bt toxins may bind to humic acids, organic supplements, or soil particles, protecting the toxins from degradation by microbes and extending the persistence of insecticidal activity in the soil (Glare & O'Callaghan 2000).

Exposure to Bt toxins via consumption of common soil-dwelling detritivores or herbivores by epigeal spiders common in agroecosystems (e.g., Lycosidae, Gnaphosidae, Linyphiidae) is likely due to their foraging habits. The presence of Bt toxins in the soil, as well as the consumption of fresh or decaying transgenic plant material, can lead to exposure of soil-dwelling organisms, such as Collembola, slugs, and earthworms (Zwahlen et al. 2003b). Collembola are readily consumed by spiders and represent a major trophic linkage; linyphiids will build their webs at micro-sites with high Collembola abundance (Harwood et al. 2001, 2003). Although spiders are capable of consuming earthworms (Nyffeler et al. 2001) and slugs (Nyffeler & Symondson 2001), these prey are not a major resource utilized by these generalist predators. Depending on the crop and agronomic aims of the grower, large amounts of crop residues may be churned into the soil during the harvesting process, allowing for further Bt toxin exposure in soil-dwelling communities, although this is not the case when all crop material is removed during harvest (e.g., corn destined for ethanol production [Giampietro et al. 1997]).

3.5 Indirect effects.—In addition to direct toxicity, the production of Bt toxins by Bt crops changes the agroecosystem relative to non-transgenic cropland in several ways that have important implications for food web dynamics. First, insertion of the gene complex into the crop plant may result in unpredicted and unintended pleiotropic effects changing the plant from its non-transgenic counterpart (Picard-Nizou et al. 1995; Saxena & Stotzky 2001; Birch et al. 2002; Faria et al. 2007). For example, a reported pleiotropic effect in Bt corn is

an increase in the lignin content of transgenic plant tissue (Saxena & Stotzky 2001), which may lead to reduced decomposition in soil (Flores et al. 2005), although other studies have shown no differences in rate of decomposition for Bt tissue (Lehman et al. 2010; Zurbrugg et al. 2010). An additional pleiotropic effect of transformation in some transgenic corn may be an increase in attractiveness as an oviposition site for corn leafhoppers *Dalbulus maidis* (DeLong & Wolcott) (Hemiptera: Cicadellidae), a pest that is not targeted by Bt toxins, possibly due to altered plant traits that influence oviposition, such as leaf vein characteristics, foliar pubescence, or plant chemistry (Virla et al. 2010). Genetic transformation of potatoes can also decrease foliar expression of toxic glycoalkaloids (Birch et al. 2002). These altered plant characteristics may impact spiders, as variations at the plant level can have effects on higher trophic levels, including predators (Lundgren et al. 2009c; Pilorget et al. 2010). How pleiotropic effects impact spiders is poorly understood, although the potential consequences of these effects merit further research.

Perhaps more importantly, prey-mediated effects of Bt crops on higher trophic levels are well documented in the laboratory (Hilbeck et al. 1998; Bernal et al. 2002b; Dutton et al. 2002; Ponsard et al. 2002; Romeis et al. 2004, 2006; Lövei & Arpaia 2005; Hilbeck & Schmidt 2006; Torres & Ruberson 2006; Naranjo 2009), although studies addressing spiders have been neglected. This multitrophic-level effect occurs when the fitness or performance of target or non-target prey that consume Bt tissue is reduced. As a result, prey may be of lesser quality or reduced abundance in Bt fields, and thus a bottom-up effect may be triggered that could affect the foraging or fitness of higher trophic levels, such as spiders (but see Torres & Ruberson 2008). Moreover, reduced prey availability may increase the likelihood that generalist predators will directly consume Bt toxins by feeding on plant-provided resources to supplement their diet (e.g., Al-Deeb et al. 2001b). Any non-neutral effects of Bt crops on spiders, whether direct or indirect, could have implications for biological control and food-web structure.

4. UPTAKE OF BT TOXINS BY SPIDERS

Despite their potential to play an important role in biological control programs and the multitude of pathways through which spiders may be exposed to Bt toxins in agroecosystems, few studies have addressed the uptake of Bt toxins in the field, as well as consequences of such exposure to spiders. Key components of non-target risk-assessment are determining the level of exposure and harm of Bt toxins, and studies involving spiders are essential.

4.1 Evidence for Bt toxin uptake by spiders in the field.— Studies documenting the presence or absence of transgenic proteins in the gut contents of spiders are scarce. Harwood et al. (2005) reported 7.7% of 91 field-collected spiders (dominated by Linyphiidae and Tetragnathidae) tested positive for Cry1Ab in field corn, indicating that exposure pathways exist for these spiders in transgenic corn. This is likely the only study in which field populations of spiders were screened for Bt toxins in a transgenic agroecosystem. Several generalist predators are better studied than spiders and regularly take up Cry1Ab in the field. These predators include ladybird beetles

(Coleoptera: Coccinellidae), ground beetles (Coleoptera: Carabidae), and damsel bugs (Hemiptera: Nabidae) (Zwahlen & Andow 2005; Obrist et al. 2006b; Harwood et al. 2005, 2007; Wei et al. 2008; Peterson et al. 2009).

4.2 Potential consequences of consuming Bt toxin.—Laboratory studies of the movement of Bt toxins through spider-based food webs, as well as the consequences of consuming these transgenic proteins on the fitness and fecundity of spider predators, are also scarce. Lövei & Arpaia (2005) point out the lack of laboratory studies using spiders, as well as several other arthropod groups, as a "striking omission" in the Bt risk-assessment literature.

Laboratory-based feeding studies examining effects of Bt toxin on spiders via consumption of non-prey resources include an orb-weaver *A. diadematus*, which showed no change in survival, weight gain, reaction time, molt frequency, or web-building when juveniles were fed Cry1Ab corn pollen via web re-ingestion (Ludy & Lang 2006a). Similarly, adults and juveniles of a tangle-web spider *Phylloneta impressa* (L. Koch 1881) (Theridiidae) fed Cry3Bb1-containing prey or pollen for eight weeks had no effect on mortality, weight gain, development, or fecundity (Meissle & Romeis 2009).

Additional studies have examined the tritrophic movement of Bt toxins into spiders via their herbivorous prey. Jiang et al. (2004) fed transgenic rice expressing Cry1Ab Bt toxins to two herbivorous insects: the striped stem borer *Chilo suppressalis* (Walker 1863) (Lepidoptera: Crambidae) and the Chinese brushbrown caterpillar *Mycalesis gotama* Moore 1857 (Lepidoptera: Nymphalidae). These prey were subsequently fed to a wolf spider, *Pirata subpiraticus* (Bösenberg & Strand 1906) (Lycosidae). Antibody assays of each trophic level indicated Bt toxins were transferred up the food chain from transgenic rice to both prey species and into the spider; however, Cry1Ab concentration diminished with each step up the food chain, and the two prey species transferred Cry1Ab up the food chain with different efficiencies (Jiang et al. 2004). Similarly, Chen et al. (2009) tracked the movement of Cry1Ab from Bt rice into *P. subpiraticus* via a leaffolder *Cnaphalocrocis medinalis* (Lepidoptera: Pyralidae). In addition to showing that Cry1Ab concentration decreased as it moved through the food chain (herbivores contained approximately 0.6–1.1 Cry1Ab/fresh weight [µg/g] and predators contained 0.06–0.12 [µg/g]), this study also demonstrated a lack of binding of Cry1Ab molecules to the mid-gut lining of *P. subpiraticus*. Although fecundity and survivorship measures were unaffected, development time was significantly longer for spiders consuming Cry1Ab-containing prey, potentially due to indirect effects of reduced prey quality (Chen et al. 2009). Delayed development could have important consequences in the field, potentially increasing predation risk, including cannibalism and intra-guild predation, which can have strong impacts on wolf spider populations (Wagner & Wise 1996; Hodge 1999). In a similar study system, Tian et al. (2010) examined the tritrophic movement of Cry1Ab from rice to herbivorous brown planthoppers *Nilaparvata lugens* (Hemiptera: Delphacidae) and their spider predators, *Ummeliata insecticeps* (Bösenberg & Strand 1906) (Linyphiidae). Cry1Ab concentration decreased as trophic level increased, with the planthopper-linyphiid uptake pathway demonstrating lower Cry1Ab mean concentrations (0.010 and 0.002 Cry1Ab/fresh weight [µg/g],

respectively) (Tian et al. 2010) than the leaffolder-wolf spider pathway (Chen et al. 2009). These differences highlight the impact prey choice can have on a spider's likelihood for Bt toxin uptake in the field. Under current commercialized Bt toxin expression systems, phloem-feeders, such as brown planthoppers are less likely to take up Bt toxins than chewing insects, such as leaffolders, and therefore may convey lower concentrations of transgenic proteins to spiders (Raps et al. 2001).

5. EFFECTS OF BT CROPS ON SPIDER ABUNDANCE AND DIVERSITY

Risk-assessment research addressing the impacts of transgenic technology on spider populations has been published for six of the most common Bt crops. These studies varied widely in many research parameters, including type of Bt toxins expressed, region where fieldwork was conducted, duration of study, sampling methods, and outcomes (Table 1).

5.1 Meta-analysis.—Meta-analyses can reveal cross-study trends in the effects of Bt crops against non-target species that are not readily apparent from examining the results of individual studies, so we used this technique to examine the effects of specific Bt crops on spider communities. Specific hypotheses tested were 1) do non-Bt crops (corn, potato, cotton, eggplant, and rice) have similar spider abundances relative to Bt-crops in the absence of insecticide use, and 2) do non-Bt crops (corn, potato, cotton) that have been treated with insecticides to manage insect pests have similar spider abundance relative to Bt crops? To address this question, we updated a database originally published by Wolfenbarger et al. (2008), which was derived from Marvier et al. (2007). Specific studies included in the current database are indicated in Table 1. The spider community was divided depending on sampling method; spiders collected with pitfall traps were distinguished from those collected with beat cloths, suction, sticky cards, whole plant counts and pan traps. The meta-analyses used Hedges' *d* as its effect size estimator (Hedges & Olkin 1985), with relative effect sizes assigned to each study based on the sample sizes, means and standard deviations of the two treatments compared. Contrasts between treatments were conducted such that a positive effect size represents a beneficial effect of the Bt crops over the non-Bt crops. Comparisons were made using MetaWin 2.1, and mean ± non-parametric bias-corrected bootstrap confidence intervals (representing 95% confidence limits) were calculated (Rosenberg et al. 2000). If the error intervals encompassed zero, the effect size was not considered to be significant. Small, medium, and large effect sizes were considered to be approximately 0.2, 0.4, and 0.6, respectively (Cohen 1988). The results of these meta-analyses are presented in Figures 2 and 3, and are discussed below.

5.2 Field corn.—Transgenic corn is the most abundant and widespread Bt crop; approximately 41 million hectares of genetically modified corn were planted worldwide in 2009 (James 2009) and 63% of all corn planted in the United States in 2010 contained at least one Bt gene (USDA NASS 2010a). Bt corn lines may express Cry1 or Cry2 Bt-endotoxins that target lepidopteran pests (primarily European corn borer *Ostrinia nubilalis* Hübner and Southwestern corn borer *Diatraea grandiosella* Dyar [Lepidoptera: Pyralidae]) and/or

Cry3 Bt-endotoxins that target coleopteran pests (corn rootworm *Diabrotica* spp. (Coleoptera: Chrysomelidae)). Due to the widespread planting of this crop, more field studies examining the impact of Bt field corn on spider abundance have been published than for any other crop.

Our meta-analyses have revealed that spider abundances are unaffected by Bt corn relative to non-Bt corn, provided that insecticides are not applied to the non-Bt fields (Fig. 2). Therefore, the planting of Bt corn as an alternative to insecticide applications may benefit spider populations. However, insecticides to control Bt-targeting pests were not applied universally prior to the adoption of Bt crops, due to annual variation in pest populations, cost of scouting for pests, and effectiveness of crop rotation in some growing areas (Smith et al. 2004). Insecticides targeting the European corn borer were applied to 7% of corn grown in the USA in 1997 (Shelton et al. 2002), and 25% of corn acreage was treated for corn rootworms in 2001 (USDA ERS 2010). For lepidopteran-targeting Cry1Ab corn, no differences in spider abundance (Pilcher et al. 1997; Lozzia & Rigamonti 1998; Lozzia et al. 1998; Lozzia 1999; Jasinski et al. 2003; Delrio et al. 2004; Daly & Buntin 2005; de la Poza et al. 2005; Eckert et al. 2006; Fernandes et al. 2007) or diversity (Volkmar & Freier 2003; Sehnal et al. 2004; Meissle & Lang 2005; Farinós et al. 2008) were found between Bt and non-Bt corn untreated with conventional insecticides, using a variety of sampling methods. Similarly, Cry3Bb1 corn had no effect on spider abundance in the absence of insecticides (Bhatti et al. 2002, 2005a; Al-Deeb & Wilde 2003). When untreated Bt corn and non-Bt plots treated with conventional insecticide applications are compared, many studies indicate significantly lower population abundance of spiders immediately following insecticide applications and season-long in the chemically treated fields than in both Cry1Ab (Dively 2005; Meissle & Lang 2005; Bruck et al. 2006) and Cry3Bb1 corn (Bhatti et al. 2002, 2005b). Seed treatments of neonicotinoids or foliar sprays of pyrethroid insecticides on both Bt and non-Bt corn also reduced spiders caught in pitfall traps (Ahmad et al. 2005). Reports of significant differences among spider populations in Bt versus non-Bt corn have often lacked consistency across growing seasons. One field study conducted in Germany reported significantly fewer spiders in Cry1Ab corn in one of the three years of the study, while there was no difference the remaining two years (Lang et al. 2005).

Determining the effect of Bt corn on individual spider species may reveal differences unseen at lower taxonomic resolution. For example, Toschki et al. (2007) reported increased activity-density of two spiders (*Bathyphantes gracilis* [Blackwall 1841] and *Tenuiphantes tenuis* [Blackwall 1852] [Linyphiidae]) and decreased activity-density in one species (*Meioneta rurestris* [C.L. Koch 1836] [Linyphiidae]) in Bt versus non-Bt corn. However, Cry1Ab corn had no effect on populations of *Oedothorax* (Linyphiidae), *Alopecosa* (Lycosidae), various tetragnathids, and juvenile linyphiids and lycosids (Candolfi et al. 2004).

When examined at the guild level, spiders grouped as "hunting" or "web-building" showed no significant differences in abundance due to Cry1Ab corn in the Czech Republic; however, populations of the family Theridiidae increased over the three year study period in conventional fields, while decreasing in Bt treatments, a result credited to temporal fluctuations in the population dynamics of these spiders (Řezáč et al. 2006). In contrast to those findings, Ludy & Lang (2006b) found that in one of the three years of their study, foliage-dwelling spiders were more abundant in Bt corn and surrounding nettle margins than in conventional fields. The same study found no significant differences in spider abundance for the remaining field seasons, as well as no difference in species richness or guild distributions based on transgenic treatment.

5.3 Sweet corn.—Some sweet corn hybrids express Cry1Ab that targets several lepidopteran pests, including European corn borer *Ostrinia nubilalis* Hübner 1796 (Pyralidae), corn earworm *Helicoverpa zea* (Boddie 1850) (Noctuidae), and fall armyworm *Spodoptera frugiperda* Smith 1797 (Noctuidae). Acreages devoted to sweet corn are small compared to field corn (0.76% of corn acres planted in the USA in 2009) (USDA NASS 2010a, b). This crop differs from field corn in having a shorter maturation rate, which allows for Bt toxins to be expressed at high levels throughout the growing season (Rose & Dively 2007). Additionally, pollen production can be three to five times greater in sweet corn than in field corn (Goss 1968, Cottrell & Yeargan 1998; Peterson et al. 2010). Therefore, trophic transfer of Bt-endotoxins via pollen consumption may play an important role in sweet corn agroecosystems.

Over the course of two growing seasons, spider abundance in pitfall traps and visual counts in transgenic and non-transgenic sweet corn plots were similar, although lambda-cyhalothrin (pyrethroid) insecticides reduced spider abundances regardless of transgenic status (Dively & Rose 2002; Rose & Dively 2007). Another study in sweet corn used vacuum sampling to measure non-target arthropod abundance; although sample sizes were low, no significant differences in abundance of spiders between transgenic and non-transgenic plots were reported for early-, mid-, and late-season plantings (Hassell & Shepard 2002). Thus, initial literature indicates that Bt sweet corn does not adversely affect the non-target spider community.

5.4 Cotton.—Bt cotton is genetically engineered to express Cry1Ac, Cry1F, Cry2Ab and/or Vip3A proteins, which target lepidopteran pests in the bollworm complex (the genera *Helicoverpa* and *Heliothis* [Noctuidae], as well as *Pectinophora* [Gelechiidae]). Genetically altered cotton is widespread; approximately 14.5 million ha of Bt cotton was planted globally in 2009 (James 2009) and in the U.S., 73% of all cotton planted in 2010 contained the Bt gene (USDA NASS 2010a). Bt cotton has significantly reduced insecticide inputs in numerous cotton-growing regions of the world, including the United States (Betz et al. 2000; Gianessi & Carpenter 1999; China (Pray et al. 2001), and South Africa (Thirtle et al. 2003). The potential impact of Bt cotton on spiders could have implications for biological control. Spiders can be important predators of key lepidopteran pests of cotton (Mansour 1987) and have been capable of maintaining pests below the economic threshold (Breene et al. 1990). For example, cursorial spiders (Anyphaenidae and Miturgidae) consume eggs and larvae of the cotton bollworm *Helicoverpa zea* (Boddie 1850) (Lepidoptera: Noctuidae) (Renouard et al. 2004; Pfannenstiel 2008).

Table 1.—Summary of literature comparing abundance and/or diversity between Bt and non-Bt crops, listed by crop, Bt toxin/s expressed, geographic region, taxonomic resolution for statistical comparisons, and sampling method/s: 1. Pitfall trapping; 2. Yellow sticky cards in foliage; 3. Visual counts; 4. Destructive sampling of corn ears; 5. Vacuum-suction sampling; 6. Beat sheet/net/bucket collection; 7. Destructive sampling of whole plant; 8. Stem elector; 9. Emergence traps; 10. Pan trapping (modified Berlese of soil and roots); 11. Sweep-netting; 12. Drop cloth sampling. Asterisks indicate the studies providing data that could be used in the meta-analyses. [a] Only collecting methods in which spiders were caught are listed.

Crop	Bt toxin/s expressed	Geographic region		Taxonomic resolution	Sampling method/s[a]	References
Field corn	Cry1Ab	North America	Iowa, USA	Arachnida	1, 2, 3	Bruck et al. 2006*
					3	Pilcher et al. 1997*
			Georgia, USA	Araneae	1, 3	Daly & Buntin 2005*
			Ohio, USA	Araneae	2	Jasinski et al. 2003*
		Europe	Germany	Araneae	3	Lang et al. 2005*
					4	Eckert et al. 2006*
				Guild, family, genus or	1	Volkmar & Freier 2003; Toschki et al. 2007
				species	5	Ludy & Lang 2006b*
					5, 6, 7, 8	Meissle & Lang 2005*
			Italy	Arachnida	2, 3	Delrio et al. 2004*
				Araneae	1, 3, 5	Lozzia & Rigamonti 1998; Lozzia et al. 1998; Lozzia 1999*
			Spain	Araneae	1, 3	de la Poza et al. 2005*
				Genus or species	1	Farinós et al. 2008*
			France	Family, genus or species	1, 6	Candolfi et al. 2004
			Hungary	Araneae	3	Árpás et al. 2005*
			Czech Republic	Guild, family or	1	Řezáč et al. 2006*
				species	1, 7	Sehnal et al. 2004*
	Cry1Ab + Vip3A	North America	Maryland, USA	Araneae	1, 2, 3, 9	Dively 2005*
		South America	Brazil	Araneae	1, 2	Fernandes et al. 2007*
	Cry3Bb1	North America	Illinois, USA	Araneae	2	Bhatti et al. 2005a*
					1, 10	Bhatti et al. 2005b
					1, 2, 10	Bhatti et al. 2002*
			Kansas, USA	Araneae	1	Al-Deeb & Wilde 2003*; Ahmad et al. 2005*
Sweet Corn	Cry1Ab	North America	Maryland, USA	Araneae	1, 2, 3	Dively & Rose 2002*; Rose & Dively 2007
			South Carolina, USA	Araneae	5	Hassell & Shepard 2002
Cotton	Cry1Ac	North America	Arizona, USA	Araneae, family or species	7, 11	Naranjo 2005*
					7	Sisterson et al. 2004*
			South Carolina, USA	Araneae	6	Turnipseed & Sullivan 1999; Hagerty et al. 2000, 2005
			Georgia, USA	Araneae	1, 12	Torres & Ruberson 2005*
				Family, genus or species	1	Torres & Ruberson 2007*
			Tennessee, USA	Araneae	11	Van Tol & Lentz 1998
			Texas, USA	Araneae	6	Armstrong et al. 2000
			Alabama, Georgia & So. Carolina, USA	Araneae	6	Moar et al. 2002; Head et al. 2005*
		Asia	Henan, China	Araneae	3	Men et al. 2003, 2004*
				Species	3	Cui & Xia 1999
		Australia	New South Wales	Family	5	Whitehouse et al. 2005*
	Cry1Ab	Australia	New South Wales	Araneae	3	Fitt et al. 1994
	Cry1Ac + Cry2Ab	North America	Arizona, USA	Araneae, family or species	1, 11	Naranjo 2005*
			So. Carolina, USA	Araneae	6	Hagerty et al. 2005*
		Australia	New South Wales	Family	5	Whitehouse et al. 2005
	Cry1Ac + Cry1F	North America	New Mexico, USA	Family, genus or species	1, 6	Bundy et al. 2005*
	Cry1Ac + Cry1Ab	Asia	Hubei, China	Araneae	3	Deng et al. 2003
	Vip3A	Australia	New South Wales	Family	3, 5, 6	Whitehouse et al. 2007*

Table 1.—Continued.

Crop	Bt toxin/s expressed		Geographic region	Taxonomic resolution	Sampling method/s[a]	References
Potato	Cry3Aa	North America	Oregon, USA	Araneae	1	Duan et al. 2004*
					6	Reed et al. 2001*
			Maryland, USA	Araneae	1	Riddick et al. 2000*
		Europe	Sofia District, Bulgaria	Species	1	Kalushkov et al. 2008
Rice	Cry1Ab	Asia	Zhejiang, China	Araneae	5	Li et al. 2007
				Species	5	Chen et al. 2009*
	Cry1Ab + Cry1Ac	Asia	Zhejiang, China	Araneae	5	Li et al. 2007
				Family	5	Liu et al. 2003
				Species	5	Liu et al. 2002
Eggplant	Cry3Bb	Europe	Basilicata, Italy	Araneae	3	Arpaia et al. 2007*

Meta-analysis revealed a slight negative effect of Bt cotton on the abundance of foliar spiders relative to non-Bt fields, but this pattern was not seen in the soil spider community (Fig. 2). Bt cotton strongly supports spider abundance when compared to non-Bt cotton with insecticide applications, which simulates normal pest management practices (Fig. 2). Individual studies comparing Bt and non-Bt cotton fields untreated with insecticides reveal differing interpretations for abundances of foliar spiders (Fitt et al. 1994; Turnipseed & Sullivan 1999; Armstrong et al. 2000; Hagerty et al. 2000, 2005; Moar et al. 2002) and similar activity-densities of epigeal spiders (Torres & Ruberson 2007). When Bt cotton is compared with insecticide-treated conventional fields, spiders are more abundant in the Bt fields (Men et al. 2004; Head et al. 2005).

However, when spider populations are examined below the ordinal level, some differences between Bt and non-Bt cotton fields arise. Spider species from multiple families, including *Hylyphantes graminicola* (Sundevall 1830) (Linyphiidae) (Cui & Xia 1999), *Emblyna reticulata* (Gertsch & Ivie 1936) (Dictynidae) and *Mecaphesa celer* (Hentz 1847) (Thomisidae) (Naranjo 2005), showed no population differences in untreated Bt and non-Bt fields. Similarly, Salticidae (Naranjo 2005) and Clubionidae (Sisterson et al. 2004) were not affected by transgenic traits; however, in one study, the remaining spider community (lumped as "other Araneae") decreased in abundance in Bt cotton (Naranjo 2005).

5.5 Potato.—Transgenic potatoes express Cry3Aa targeting the Colorado potato beetle *Leptinotarsa decemlineata* Say 1824 (Coleoptera: Chrysomelidae), which is capable of decimating potato crops and costing farmers millions of dollars per year (Perlak et al. 1993; Kalushkov et al. 2008). Bt potatoes were grown commercially in the United States starting in 1995, but were withdrawn from the market in 2001 following pressure from anti-biotechnology groups and the lack of markets for Bt potato products (Kaniewski & Thomas 2004). However, this crop may see a resurgence in planting in Russia and eastern Europe in the near future (James 2009), as need for alternatives to costly insecticides for small-scale and subsistence farmers in these areas is great (Kaniewski & Thomas 2004). The spider community can dominate the epigeal predator fauna in potato fields (comprising up to 23% of total pitfall catches, second only to Collembola) (Duan et al. 2004), and may therefore play an important role in potato agroecosystems, highlighting the importance of assessing the impact of Bt potatoes on the spider community.

Although there were very few published studies on this topic, Bt potatoes tend to favor spider populations whether the non-Bt fields are sprayed with insecticides or not (Fig. 2). The adoption of Bt potatoes causes only a minor reduction in insecticidal applications, due to pest pressure from numerous species in addition to Bt-targeted Colorado potato beetles (Betz et al. 2000). As observed in previous crops, spraying non-Bt potatoes with insecticides has more of an impact on spider populations than Bt potatoes do (Riddick et al. 2000; Reed et al. 2001; Duan et al. 2004). However, Kalushkov et al. (2008) showed no significant differences in activity-density of spider species or community composition (measured by Sørensen similarity index) in response to insecticidal treatments or Bt potatoes. A similar meta-analysis to the one we ran on the abundance of non-target arthropods reported a positive effect of Bt potatoes on piercing/sucking insects, as well as generalist predators as a whole when compared to non-Bt potatoes (Cloutier et al. 2008). These authors believed that the increase in potential prey items was driving the increase in generalist predator populations.

5.6 Rice.—This crop has been engineered to express Cry1Ac and/or Cry1Ab for the control of several lepidopteran pests, including the striped stem borer *C. suppressalis* (Crambidae), yellow stem borer *Scirpophaga incertulas* (Walker 1863) (Pyralidae), and the leaffolder *Cnaphalocrocis medinalis* (Guenée 1854) (Pyralidae) (High et al. 2004; Wang & Johnston 2007). Although field trials with Bt rice have been conducted in China since 1998 (Tu et al. 2000), most transgenic lines are not yet commercially available. Agronomic practices in rice, such as periodic flooding of cultivated fields, shapes the insect community; in irrigated fields, up to 90% of arthropod diversity may be represented by freshwater species (Schoenly et al. 1998). Despite this, spiders have a long history of use in biological control programs in rice (e.g., Oraze et al. 1988; Heong et al. 1991; Sigsgaard 2007; Way & Heong 2009).

Our meta-analysis revealed a deleterious effect of Bt rice on spider abundance relative to non-Bt paddies (Fig. 2) (Chen et al. 2009). However, other field studies in China have found similar spider abundances in Bt and non-Bt rice paddies (Liu et al. 2002, 2003; Li et al. 2007). Additionally, Tian et al. (2010) focused on the population dynamics of the spider species *U. insecticeps* for three years in Bt and non-Bt rice

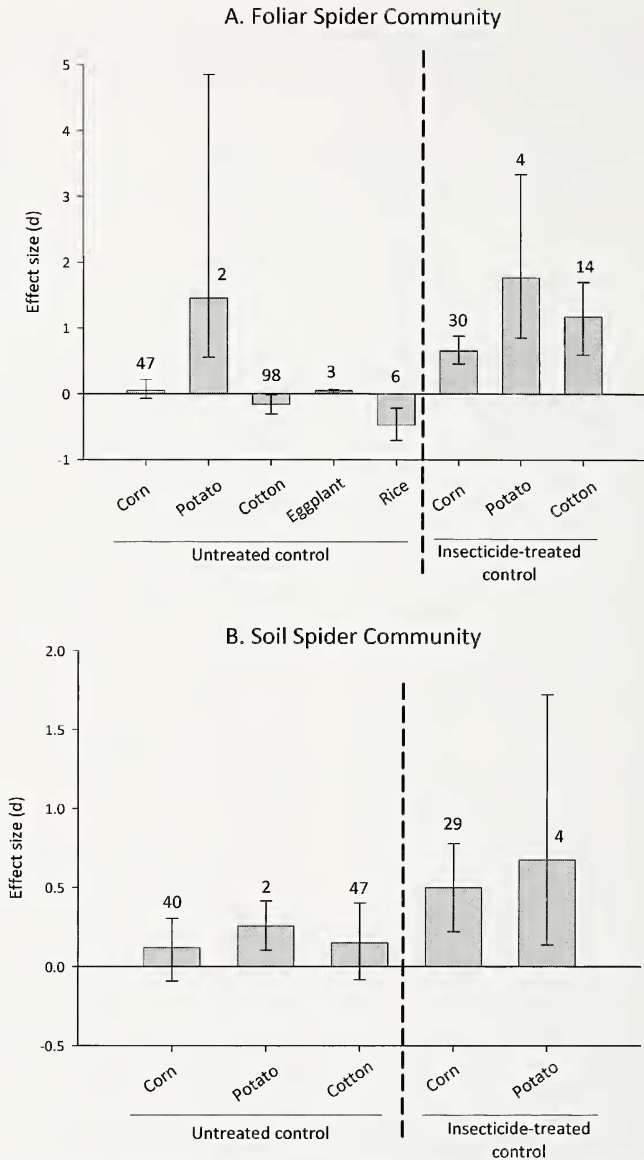## A. Foliar Spider Community

B. Soil Spider Community

Figure 2.—The effects of Bt crops on foliar (A) and soil (B) communities of spiders, relative to insecticide-treated and untreated non-Bt controls. Positive bars indicate those crops in which spider abundance is favored by Bt treatment, and negative bars are crops in which spiders are less abundant in Bt-fields. Error lines represent biased 95% confidence intervals, and the numbers of observations for each system are noted above each bar.
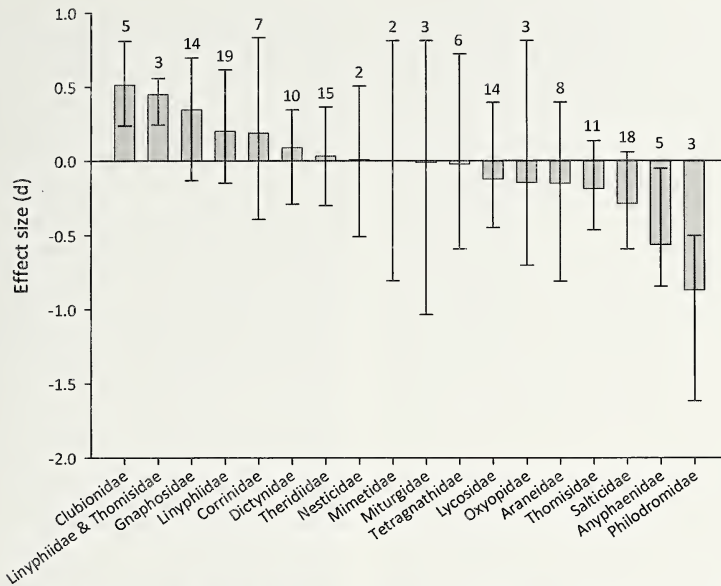
Figure 3.—The effects of Bt crops on spider families. Bars represent the effect sizes of Bt fields relative to non-Bt control fields that received no insecticides. Positive bars indicate those families favored by Bt treatment, and negative bars are families less abundant in Bt-fields. Error lines represent biased 95% confidence intervals, and the numbers of observations for each family are noted above each bar.

fields, reporting no differences for this predator; this linyphiid builds webs at the bottom of rice plants and is a major predator of the brown planthopper, *Nilaparvata lugens* (Stål 1854) (Hemiptera: Delphacidae) (Tian et al. 2010).

5.7 Eggplant.—Although the major contributors to Bt crop acreage worldwide are corn and cotton, other insect-resistant crops on the verge of commercialization, such as eggplant, could potentially see increased planting in the near future, particularly in India, where eggplant is a staple food (James 2009). Our meta-analysis revealed a slight, but significant positive effect of Bt eggplant over non-Bt eggplant (Fig 2). However, this analysis was based on a single study (Arpaia et al. 2007). Further research on the impact of Bt eggplant on spiders is necessary, particularly since the worldwide acreage of this crop may increase dramatically in the near future.

5.8 Other crops.—Additional Bt crops include oilseed rape (canola) (Stewart et al. 1996), tomato (Mandaokar et al. 2000), broccoli (Chen et al. 2008), collards (Cao et al. 2005), chickpea (Acharjee et al. 2010), spinach (Bao et al. 2009), soybean (Miklos et al. 2007), tobacco and cauliflower (Kuvshinov et al. 2001). However, these crops are not available commercially and are therefore very limited in their global planting. Despite some studies examining risk-assessment of these crops to non-target herbivores and natural enemies (e.g., Ferry et al. 2006; Chen et al. 2008; Romeis et al. 2009), no data exist for impact on spider populations in these transgenic agroecosystems.

5.9 Summary.—The spider risk-assessment literature is dominated by field studies conducted in the United States (48% of total references), Western Europe (23%), and China (15%). Studies in corn represent field sites in the U.S. and Europe, with just a single study from South America (Fernandes et al. 2007). Although Bt corn is grown in additional areas globally, such as Canada, South Africa, Egypt, and the Philippines (James 2009), these regions are not represented in the spider risk-assessment literature.

Overall, there was no consistent effect of Bt crops on spider abundance relative to non-Bt crops (Effect size = 0.01; 95% CIs ± 0.07; n = 268), but insecticides consistently have a greater negative effect on spiders than Bt crops do (Effect size = 0.73; 95% CIs ± 0.18; n = 81). However, a lack of taxonomic resolution, potentially biased methods of sampling, and a scarcity of studies in key geographic regions and crop types limits the completeness of the literature on this subject.

6. DISCUSSION

The existing risk-assessment literature allows some conclusions to be made on the effect of Bt crops on the spider community, which are predominantly non-negative. However, there are several limitations of these studies, including the lack of taxonomic resolution, use of collection techniques that may alter the perception of dominance within spider communities, and the variation in spider populations possibly due to crop type.

6.1 Interactions of Bt crops with spiders are often, but not always, neutral.—Bt crops can express one or multiple toxins that target a range of pests and are found in differing concentrations and distributions throughout the plant. This complexity, combined with the functional diversity of spiders and their often-intricate food webs, complicates the ability to make definite conclusions concerning the long-term effects of Bt crops on spiders. However, for the two most well-studied crops, corn and cotton, spiders appear to experience no direct negative effects from the adoption of Bt technology. Meta-analysis reveals no significant differences for total abundance of foliar and epigeal spiders when insecticides are absent, and spider abundance is more severely reduced when chemical applications are made than when Bt crops are planted without insecticides (Fig. 2). In contrast, the lesser-studied crops indicate non-neutral effects: Bt rice has fewer foliar spiders than non-Bt fields, while populations of soil and foliar spiders are greater in Bt potato (Fig. 2; but note the small number of observations in both of these systems). Also, some taxa within the Araneae (Anyphaenidae and Philodromidae) are adversely affected by Bt crops (Fig. 3).

The reasons for decreased spider abundance in rice and within certain taxa are not known, but it seems likely that these effects may be related to reductions in prey quality rather than direct toxicity of Bt proteins to spiders (Chen et al. 2009). Bt toxins are lethal to targeted pest species and cause the removal of those organisms from the agroecosystem; certain life stages of targeted pests are no longer available as potential prey items. Anyphaenids and philodromids are common in crops, such as cotton, where they are active foliar hunters most often collected by sweep-netting or beat sheet methods (Bundy et al. 2005). These families consume soft-bodied prey (Renouard et al. 2004; Pfannenstiel 2008), including Lepidoptera, which are targeted by the toxins expressed in Bt cotton. The absence of lepidopteran prey or their reduced quality due to feeding on Bt toxins may account for the observed negative effects of Bt crops on the families Anyphaenidae and Philodromidae (Fig. 3).

6.2 Greater taxonomic resolution is needed to reveal differential impacts of toxins on spiders.—Spiders are a diverse and abundant group within the predator community of Bt field crops (Duan et al. 2004; Sisterson et al. 2004; de la Poza et al. 2005). However, despite their prominent role, spiders have frequently been lumped into a single group at the order level for risk-assessment analysis (e.g., Fitt et al. 1994; Lozzia et al. 1998; Lozzia 1999; Turnipseed & Sullivan 1999; Armstrong et al. 2000; Reed et al. 2001; Bhatti et al. 2002, 2005a,b; Hassell & Shepard 2002; Deng et al. 2003; Duan et al. 2004; Ahmad et al. 2005; Daly & Buntin 2005; Eckert et al. 2006; Arpaia et al. 2007). The results of these studies are limited by their lack of taxonomic resolution. Spider communities occupy many functional niches, allowing for the ecological changes associated with Bt crops to affect spider species differentially. Studies of non-target impacts may reveal differences among treatments when data are examined in further taxonomic detail. For example, significant differences in the populations of several spider species in Bt vs. non-Bt crops were found when identified at greater taxonomic resolution (Naranjo 2005; Řezáč et al. 2006; Toschki et al. 2007).

Knowledge of the differential impact of insecticides on the abundance and fitness of spiders supports the hypothesis that Bt toxins will not affect spider species identically. For example, populations of a sheet weaver *Oedothorax apicatus* (Blackwall 1850) (Linyphiidae) responded negatively to applications of a pyrethroid insecticide, while a wolf spider (*Alopecosa* sp.) population was unaffected (Candolfi et al. 2004). Interactions of insecticides with spiders indicate both species- and insecticide-specific susceptibility, with frequent lethal (e.g., Fountain et al. 2007; Pekár & Beneš 2008) and sub-lethal effects (e.g., Deng et al. 2006; Tietjen & Cady 2007; Řezáč et al. 2010). Spider species also show differences in their susceptibility to certain chemical insecticides in the field; for example, populations of web-building spiders (Theridiidae) are less sensitive to certain types of insecticidal applications than ambush hunters (Philodromidae) (Bostanian et al. 1984). Susceptibility to insecticides is influenced by foraging mode, diel activity patterns, and web structure of spiders; one study found diurnal hunters and orb-web weavers were most susceptible to insecticides in the field (Pekár 1999). By extrapolating the results of the impact of other insecticidal products to the potential impact of transgenic Bt toxins on spiders, a pattern emerges. Individual spider species may be differentially affected, although it is important to note that Bt proteins are known to have a narrower range of toxicity than traditional insecticides.

We looked for patterns in the effects of Bt on different spider families, using a meta-analysis (using methods described above). The abundances of specific families in Bt versus non-Bt crops (without insecticides) vary substantially, suggesting that family-level effects of Bt crops are likely occurring but are being overlooked when spiders are grouped at the ordinal level (Fig. 3). These results highlight the need for specific study of spiders filling diverse and unique niches within an agroecosystem: large guild-level analyses grouping spiders into overly simplified groups may prevent any meaningful observation of treatment-level effects. It is therefore essential to study spiders in taxonomic detail, so that elucidation of potential differences among spider species is possible.

6.3 Collection techniques affect the perception of dominance within spider communities.—Sampling method strongly affects the number, diversity, and type of spiders collected (Amalin et al. 2001). Ecological traits of spider species, such as retreating behavior, can influence which collecting methods will be most effective. For example, wandering spiders using concealed retreats constructed from folded leaves and sticky silk (Anyphaenidae, Miturgidae) are easily observed visually, but are difficult to collect via methods such as vacuum-sampling or beat sheets that attempt to dislodge spiders from the habitat (Amalin et al. 2001). Therefore, the collecting method utilized by researchers in examining the spider communities in Bt versus non-Bt crops is likely to affect the results of these field studies.

Sampling methods varied widely within the non-target organism risk-assessment literature, although pitfall trapping was frequently used as a means to collect epigeal spiders and was often the only collection method utilized for spider capture (e.g., Riddick et al. 2000; Al-Deeb & Wilde 2003; Volkmar & Freier 2003; Duan et al. 2004; Ahmad et al. 2005;

Řezáč et al. 2006; Torres & Ruberson 2007; Toschki et al. 2007; Farinós et al. 2008; Kalushkov et al. 2008). Although pitfall trapping is recognized as measuring activity-density rather than absolute density (Thiele 1977), this method is often chosen for its low cost and high capture efficiency (Topping & Sunderland 1992). However, pitfall trapping alone has been noted as a poor indicator of overall abundance, as well as relative abundance of epigeal predators in arable land, often overestimating certain groups (e.g., Lycosidae) and underestimating others (e.g., Linyphiidae) (Lang 2000). Moreover, predator communities captured in pitfall traps are poorly correlated with predation intensity observed in these habitats (Lundgren et al. 2006). Additional characteristics of pitfalls may also affect the efficiency and composition of arthropods captured, including sampling effort (number and duration of pitfall trapping) (Riecken 1999), sampling interval (Schirmel et al. 2010), type of preservative used (Curtis 1980), use of fencing (Holland & Smith 1999), and diameter of pitfall traps (Brennan et al. 2005).

Collection methods for foliar-based spiders included yellow sticky traps, visual searching, whole plant destructive sampling, sweep netting, beat sheet collection, and vacuum-sampling (DVAC suction sampling). Risk-assessment studies in cotton in particular tend to focus on the foliar-based spiders only by using these methods and not epigeal collection methods (e.g., Van Tol & Lentz 1998; Turnipseed & Sullivan 1999; Armstrong et al. 2000; Hagerty et al. 2000, 2005; Moar et al. 2002; Head et al. 2005; Whitehouse et al. 2005); this type of sampling likely skews the data in favor of aerial web-building and foliage-adapted hunting spiders (e.g., Araneidae, Anyphaenidae, Miturgidae) and completely ignores other ground-based web-builders and epigeal hunters (e.g., Linyphiidae, Lycosidae).

Meissle & Lang (2005) determined that the most efficient collecting method for foliar spiders in corn was vacuum-suction sampling, collecting the greatest number and diversity of spiders, plus allowing for lower variation between samples, leading to increased statistical power. In contrast, Amalin et al. (2001) found vacuum-sampling was the least effective sampling method for collecting spiders, particularly for hunting spiders, and spider guilds were not equally collected using this technique. Vacuum-suction sampling has also been found to be an effective collection method of spiders in natural grasslands, although increased vegetation height decreased collection efficiency (Brook et al. 2008); this limitation could have implications for collecting, depending on crop plant architecture.

Our meta-analysis revealed that soil-dwelling and foliar spider communities responded differently to Bt and non-Bt crops in several situations (Fig. 2). Ultimately, using multiple collection methods allows for a more complete examination of the spider community. For example, one study including both foliar and epigeal collections reported a higher mean abundance of spiders based on sweep-net samples, but no significant differences between mean abundances collected by pitfall trapping (Torres & Ruberson 2005). This may indicate that spatial distribution and/or functional niche within an agroecosystem may impact the way that transgenic crops affect subsets of the spider community. Non-target risk-assessment studies of spiders should therefore employ multiple collection methods and get identifications in greater taxonomic detail to obtain an accurate picture of the ecological processes at hand. In some cases, the sampling methods used to collect spiders may affect the ability to detect potential differences in populations between Bt and non-Bt crops. A combination of multiple collection techniques is recommended for the most accurate sampling of spider communities.

6.4 Spider population trends vary spatially and temporally within agroecosystems, and these dynamics are strongly influenced by the crop.—The distribution and expression levels of Bt proteins within a transgenic plant vary depending on the type of Bt toxin, transformation event, gene promoter used, developmental stage, crop phenology, and environmental and geographical effects (Lundgren et al. 2009a). Although the crop plants reviewed here all express Bt toxins, they vary widely in other biological aspects, such as habitat structure and complexity, plant phenology, availability of non-prey resources, microclimatic conditions, and level of disturbance. Therefore, we can predict that the spider communities within each crop type will vary. Uetz et al. (1999) reported differences in the structure of spider guilds within crop fields in the United States. This study presented two distinct dominance structures: those dominated by the guilds defined as "ground runners" (Lycosidae, Dysderidae, and Gnaphosidae) and "web-wanderers" (Linyphiidae and Micryphantidae), which included rice, as well as those crops dominated by "orb weavers" (Araneidae, Tetragnathidae, and Uloboridae) and "stalkers" (Mimetidae, Oxyopidae, and Salticidae), which included corn and cotton. Inherent differences in the spider communities in distinct cropping systems may lead to differential effects of Bt crops on spider assemblages.

7. CONCLUSIONS

Spiders are some of the most diverse and abundant predators in field cropping systems, although their diversity and idiosyncrasies are currently lost in most studies examining Bt crops. Spiders have received little attention in proportion to their abundance and importance as generalist predators in agroecosystems. By combining all spiders together in the analysis of such studies, the ecological value of the data is lost and the potentially differential impact of Bt crops on functionally distinct spider species is subverted. It is therefore essential for risk-assessment literature examining impacts on spiders to identify them to the lowest taxon possible, in order to elucidate how Bt crops are impacting the diverse assemblages of Araneae in transgenic agroecosystems.

Although there are many mechanisms through which Bt crops could affect spiders, there are no consistent negative effects observed in the literature on toxicity of Bt toxins against them. Further study on the uptake of Bt toxins by spiders, pathways to exposure, and the consequences of such are necessary to further our understanding of the interactions between Bt crops and spider assemblages. A remaining question is how Bt-crop-associated changes to agroecosystems affect the ability of spider communities to regulate pest populations.

Several caveats to approaches to sampling spider communities challenge our interpretation of current data involving Bt non-target studies. These include the sampling approach

selected, as well as the region and duration of sampling applied. The diversity of the spider community creates challenges for accurately estimating population densities and can alter perceptions of dominance within spider species assemblages. A multi-tactic strategy will likely give us the best understanding of spider communities within agroecosystems.

Transgenic crop technology has been rapidly adopted in many countries and continues to increase in its planting worldwide. Current transgenic crop development has focused on both the stacking (expression of more than one type of transgene product that target multiple pest species) and pyramiding (expression of more than one type of transgene product that target the same pest) of genes. With the adoption of new crops and expression of additional Bt toxins, risk-assessment is increasingly necessary in understanding how biotechnology may affect ecologically important groups of organisms, such as spiders.

8. ACKNOWLEDGMENTS

9. LITERATURE CITED

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